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Temporal assemblage turnovers of intertidal foraminiferal communities from tropical (SE Caribbean) and temperate (NE England and SW Spain) regions

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ABSTRACT

This is the first quantitative study of temporal assemblage turnovers of the relationships between intertidal foraminifera. Time series datasets collected from tropical Caroni Swamp and Claxton Bay (Trinidad, SE Caribbean) and temperate Cowpen Marsh (NE England, U.K.) and Bay of Cadiz (SW Spain) were used. The assemblage turnover index (ATI) examined species interrelationships through comparisons of monthly or biweekly species proportional abundances over one or two years. Species contributing to major assemblage turnovers (ATI > x + σ) were identified using the conditioned on-boundary index (CoBI). Foraminiferal species are heterogeneously distributed within the sediment; multiple sample stations at a study location cumulatively represent the foraminiferal metacommunity and clusters represent foraminiferal assemblages. The ATI and CoBI were applied to the proportional abundances of live specimens recorded for the metacommunity and assemblages at each location. At Caroni Swamp and Claxton Bay, major assemblage turnovers were driven by the most abundant species and the majority coincided with seasonal change or the arrival of the seasonal Orinoco plume in the Gulf of Paria. Seasonal turnovers of the foraminiferal metacommunities at temperate Cowpen Marsh and Bay of Cádiz occurred during the summer and winter. Major assemblage turnovers in the upper Cowpen Marsh occurred in the summer, and the lower marsh in the winter. Foraminiferans are useful bioindicators for monitoring the health of coastal environments. Understanding foraminiferal population dynamics will allow cyclical changes to be differentiated from abrupt and persistent changes, which are related to anthropogenic disturbances or long-term climate change. The ATI and CoBI are useful indices for quantitatively exploring relationships of foraminiferal populations over time.

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1. Introduction

Benthonic foraminifera are useful bioindicators for monitoring marine environments to detect pollution or long-term climate change (Scott et al., 2001). Research on the use of foraminifera as bioindicators, initiated by Resig (1960) and Watkins (1961), is still in its developmental stage (Martinez-Colón et al., 2009). Natural variability, such as seasonal patterns in foraminiferal population dynamics, should be differentiated from regime shifts, which are abrupt and persistent changes that signify alteration of the environment (Murray and Alve, 2000). Time series studies are uncommon because of the greater time, physical and monetary requirements to complete. A superior understanding of natural variability can be extracted from time series data sets through various analyses. A novel approach is the assemblage turnover index (ATI) and conditioned on-boundary index (CoBI) which use species proportional abundances to compare species relationships over time (Hayek and Wilson, 2013). Major assemblage turnovers and the species that contributed can be determined to coincide

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with seasonal change and species fluctuations would indicate ecological patterns. This study is the first to examine quantitatively temporal foraminiferal assemblage turnovers by applying ATI and CoBI to time series datasets collected from four intertidal environments exposed to different (tropical and temperate) seasonal patterns.

The majority of time series studies have been conducted at temperate latitudes, where annual and intra-annual cyclicity of species diversity and biomass has been recorded (e.g., Swallow, 2000; Murray and Alve, 2000; Alve and Murray, 2001). At temperate latitudes, population blooms usually occur in the warmer months and are commonly ascribed to increased food supply from phytoplanktonic or microalgal blooms. The system is chaotic; patterns observed one year are not always precisely reproduced in the following year or between stations at the same location (Buzas et al., 2015). Fewer studies of foraminiferal time series have been conducted at tropical latitudes (Buzas et al., 1977; Wilson and Horton, 2012; Tedesco and Thunell, 2003; Costelloe and Wilson, 2015, 2017). Seasonal population blooms, species dominance and diversity have been recorded at some locations (Tedesco and Thunell, 2003; Debenay et al., 2004; Wilson, 2010; Costelloe and Wilson, 2015) but not others (Buzas et al., 1977). Buzas et al. (1977) monitored foraminiferal communities of tropical *Thalassia* environments in the northern Caribbean region and suggested biotic controls, such as competition, were more influential than abiotic variables, which were more consistent at tropical latitudes. Population dynamics governed by biotic controls is better examined through species proportional abundances because species fluctuations relative to others are missed by using absolute densities. The ATI and CoBI indices offer this advantage and have not been previously used to detect quantitatively temporal assemblage turnovers of live foraminiferal communities.

The data sets used here from tropical sites, Caroni Swamp (NW Trinidad) and Claxton Bay (SW Trinidad), and temperate sites Cowpen Marsh (NE England) and Bay of Cádiz (SW Spain), were first reported by Costelloe and Wilson (2015, 2017), Horton (1999) and Papaspyrou et al. (2013). Such time series data sets are rare (others include Basson and Murray, 1995, Swallow, 2000, Alve and Murray, 2001 and Buzas et al., 2002). At the chosen locations, seasonal population dynamics have been suggested through previous work by the authors. These locations are suitable for an initial application of the ATI and CoBI approach to detecting assemblage turnovers in intertidal foraminiferal communities that coincide with both tropical and temperate seasonal patterns. The data sets are not identical so the results are not statistically comparable, but patterns in assemblage turnovers are separately noted for each location.

2. Study area

Caroni Swamp is located 35 km north of Claxton Bay on the west coast of Trinidad (SW Caribbean) that opens to the Gulf of Paria, a shallow semi-enclosed embayment that separates Trinidad from north eastern Venezuela. Caroni Swamp is a 60 km^2 mangrove wetland reserve and Claxton Bay is a 2.25 km-long stretch of mangrove shoreline in an industrial area. Both experience semi-diurnal tides and a tidal range of approximately 1 m. Three sample sites at Caroni Swamp are located near the coastline and mouth of the Blue River. Sites 1 and 2 are less than 15 m apart and ~25 m inland from the coastline, and Site 3 is ~1 km upstream of site 2 (Costelloe and Wilson, 2017). At Claxton Bay, site 1 was adjacent to a cement factory and rivulet along the coastal edge of the mangrove. Trinidad's proximal location to the equator produces two opposing seasons. Rainfall is traditionally lowest between January and May (dry season) than June to December (wet season) when a meridional shift in the intertropical convergence zone (ITCZ) results in heavier rainfall. Late May and December are considered transitional periods between the seasons. The Orinoco Delta (NE Venezuela) is approximately 20 km south of the south-western coast of Trinidad. River discharge is seven times greater in a wet season, from June to December, than in a dry season, from January to May (Hu et al., 2004). Fluvial discharge from the Orinoco River is carried through the Gulf of Paria by the Guyana Current (Corredor and Morrel, 2001) creating a plume that typically exceeds 160,000 km^2 of the Caribbean Sea (Hu et al., 2004). The low salinity Orinoco plume is a marked feature of the Trinidad wet season.

Cowpen Marsh is a 400 m-wide tidal flat in the western Tees Estuary, NE England. It has a macro tidal range between 6 and 4.6 m. Bay of Cádiz (SW Spain) is a 38 km^2 protected reserve comprised of a shallower inner bay connected by the Puntales Channel to a deeper outer bay on the south western coast of the Iberian Peninsula. The Bay experiences semi-diurnal tides with a range of approximately 1.24 m. Seasonality is characterized by colder and wetter autumn (September to November) and winter (December to February) months when salinity is lower, and warmer and dryer spring (March to May) and summer (June to August) months when salinity is higher (Papaspyrou et al., 2013). Spring and summer blooms in foraminiferal populations have been recorded at several temperate marshes (Alve and Murray, 1994; Murray, 1983; Murray and Alve, 2000; Swallow, 2000) and at Cowpen Marsh (Horton, 1999) and Bay of Cádiz (Papaspyrou et al., 2013). Species dominance can change between months (Daniels, 1970; Wefer, 1976; Jones and Ross, 1979; Debenay et al., 2004), and seasonal assemblage turnovers may occur due to subdominant species opportunistically capitalizing on resources during unfavorable months.

3. Materials and methods

3.1. Sampling

Caroni Swamp and Claxton Bay were sampled monthly from March 2011 to May 2013 and July 2012 to 2013 at three and one sites, respectively. Sample stations were placed at high (A), mid (B) and lower (C) elevations at each site (Table 1). Four replicated sediment samples (75 $cm^2 \times 1$ cm) were collected at each station and counted separately, but for further analyses the counts from each replicate were summed and reflect 300 cm^3 of sediment at each station. Cowpen Marsh was sampled biweekly from 1st May 1995 to 3rd May 1996 at 31 stations along a 200 m transect (Table 1). On each occasion, one sediment sample (10 $cm^2 \times 1$ cm) was collected at each station. The inner Bay of Cádiz was sampled monthly from July 2008 to June 2009 (with the exception of August 2008 and April 2009) from three 1 m^2 plots placed 10–15 m adjacent to each other (Table 1). Three replicated sediment samples (2 $cm^2 \times 10$ cm) were taken, such that 60 cm^3 of sediment was collected from each plot.

All sediment samples were soaked in a solution of alcohol and the protein stain rose bengal to allow identification of foraminiferans which were live at the time of sampling (Walton, 1952). Samples were washed through a 63 μm sieve. Specimens were picked wet and counted from the entire >63 μm fraction of samples from Caroni Swamp and Bay of Cádiz, but samples from Claxton Bay and Cowpen Marsh were split using a wet splitter into 1/16 and 1/8 aliquots, respectively. The taxonomy followed Todd and Bronnimann (1957) for Caroni Swamp and Claxton Bay; Murray (1971, 1979) and De Rijk (1995) for Cowpen Marsh; and Loeblich and Tappan (1987) for Bay of Cádiz.

Table 1
Elevation of stations (STN) at Caroni Swamp, Claxton Bay, Cowpen Marsh; and plots at Bay of Cadiz.

Tropical study locations						Temperate study locations					
Caroni swamp			Claxton bay			Cowpen Marsh			Bay of Cadiz		
Site	STN	Elevation (m, above mean sea level)	Site	STN	Elevation (m, above mean sea level)	Site	STN	Elevation (m, above Ordinance Datum)	Site	Plot	Elevation (m, above hydrographic zero)
10°36′21.70535″ N 61°29′06.85971″ W	1A	0.655	10°20′56.17158″ N 61°27′45.54136″ W	1A	0.228	54°37′18″N, 1°13′29″W	15	3.24	39° 31 ′ 09 ″ N 6° 12 ′ 01 ″ W	I	1.5–1.7
	1B	0.453					610	2.42			
	1C	−0.176					11	2.18			
							−15				
	2A	1.487					16	2.04			
	2B	0.195					17	1.99			
							−20				
	2C	−0.051		1B	0.051		21	1.52		II	
							22	1.32			
10°36′39.14429″N 61°28′57.29060″ W	3A	−0.14					23	1.13			
							24	0.93			
	3B	−0.102					25	0.72			
							26	0.54			
				1C	−0.151		27	0.36		III	
	3C	−0.117					28	0.17			
							29	−0.04			
							30	−0.22			
							31	−0.35			

3.2. Cluster analysis

Along the tidal frame, calcareous and agglutinated species dominate lower and higher elevations, respectively (Sen Gupta, 1999). This heterogeneous distribution of species splits the foraminiferal metacommunity into assemblages. Metacommunities and assemblages are examined at each location since population dynamics may vary between (Swallow, 2000; Murray and Alve, 2000). Q-mode cluster analysis defines foraminiferal assemblages by using either the total (live + dead) or dead counts recorded from a single sample occasion. Authors may disagree concerning the use of either total (Buzas, 1968; Scott and Medioli, 1980; Scott and Leckie, 1990; Jennings et al., 1995; De Rijk, 1995; Scott et al., 2001) or dead counts (Murray, 1982, 1991, 2000) to define assemblages. Because the dead tests accumulate over time, most authors agree that the inclusion of dead tests allows for averaging annual conditions over a time series. Q-mode cluster analysis of the total (N_T) or dead (N_D) counts recorded from the sample occasion with the highest recovery, is used to provide an assemblage scheme and applied across the entire time series. Within the spatial boundaries of the defined assemblage scheme at each location, analysis of the live counts (specimens stained by rose Bengal) highlights temporal change since these represent conditions at the time of sampling (Buzas, 1968; Murray, 1982).

Previous work by Costelloe and Wilson (2015, 2017) defined two assemblages at Caroni Swamp, Claxton Bay using N_T and Cowpen Marsh using N_D (Table 2). Q-mode cluster analyses of months with the highest recovery were used: May 2012 at Caroni Swamp; May 2013 at Claxton Bay; and August 10, 1995 at Cowpen Marsh. Caroni Swamp and Claxton Bay assemblages (denoted by I, II and III) were not constrained by elevation due to seasonal flooding (Costelloe and Wilson, 2017). However, the respective species compositions of assemblages I, II and III are comparable to those constrained between high, mid and lower tidal elevations by Wilson et al. (2008). This relationship was demonstrated by performing Q-mode cluster analysis of Caroni Swamp and Claxton Bay samples in conjunction with those of Wilson et al. (2008). For this reason, N_T from Caroni Swamp and Claxton Bay were used in cluster analysis to follow the methods of Wilson et al. (2008). The authors confirm that a similar assemblage scheme is derived by using N_D, either in conjunction with samples of Wilson et al. (2008) or separately. For cluster analysis of Cowpen Marsh samples, N_D were used since Horton (1999) suggested these best represent average annual conditions. At Bay of Cádiz the entire tidal range was not sampled because all three sample plots were adjacent to each between 1.5 and 1.7 m above hydrographic zero. Instead the plots were examined together (summed) as a representation of the metacommunity; and separately to detect any inconsistencies between the temporal population dynamics between plots.

3.3. Assemblage turnover index (ATI)

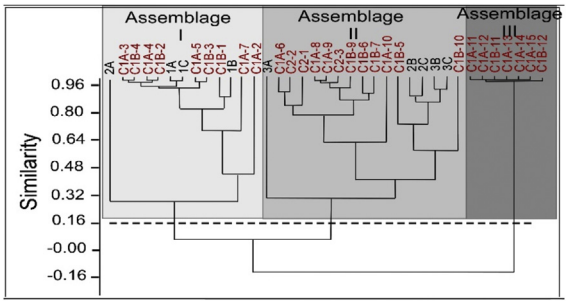
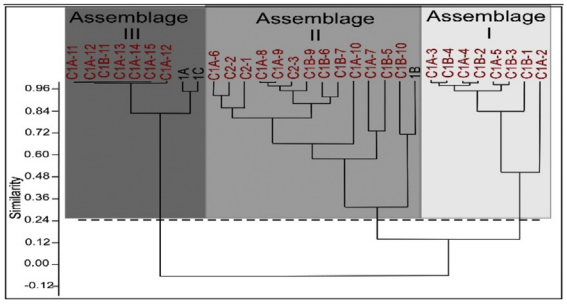
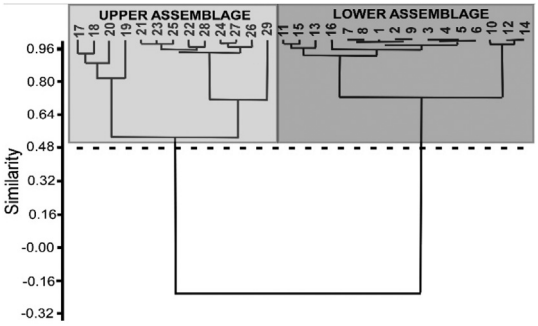
The ATI compares species proportional abundances between samples, referred to as sample-wise ATI values (ATI_s). The CoBI identifies the proportional contribution of each species to peak values of ATI_s. Hayek and Wilson (2013) provide the analyst with two forms of CoBI, partial-CoBI ($CoBI_p$) and thorough CoBI ($CoBI_t$). The former examines species contributions immediately at PATI boundaries and the latter examines that between entire PATI intervals. In this way, $CoBI_p$ allows the analyst to detect species which lead the change at PATI boundaries, and $CoBI_t$ describes the change in species proportional abundances between the assemblages within PATIs.

Species abundances were converted to proportional abundances (p_i). For each species, the p_i of the first sample occasion (p_{i1}) was subtracted from the second sample occasion (p_{i2}). This was done pairwise over contiguous samples for all successive sample occasions. Sample-wise ATI values (ATI_s) for each sample occasion was the sum of all absolute values of p_{i2} - pi_1 (Eq. (1); Hayek and Wilson, 2013), such that

$$ATI_s = \sum |p_{i2} - p_{i1}| \quad (1)$$

The mean, x, and standard deviation, σ, of all ATI_s values over the entire time series were calculated. Temporal boundaries were drawn at peaks in ATI_s values, where $ATI_s > x + \sigma$. Peaks in ATI_s indicate major assemblage turnovers. The interval of time between peak ATI_s values is referred to as peak-bounded ATI intervals

Table 2
Foraminiferal assemblages defined at Caroni Swamp, Claxton Bay and Cowpen Marsh using Q-mode cluster analysis. At Bay of Cádiz, the assemblage of adjacent plots placed at similar tidal elevations were examined seperatley and collectively without cluster analysis.

Location	Assemblage	STN	N	Species Richness	Species recovery >10%	Q-mode Cluster Analysis (Wilson et al., 2008 samples depicted in red)
Caroni Swamp (N_T recorded on May 2012)	I	2A 1A 1B 1C	1121	17	*Arenoparella mexicana* (56%) *Trochammina inflata* (19%) *Trochammina advena (11%)*	
	II	2B 2C 3A 3B 3C	1748	15	*Ammotium salsum* (41%) *Triloculina trigonula* (15%) *Lagena* sp. (14%) *Trochammina advena* (11%)	
Claxton Bay (N_T recorded on May 2013)	II	1B	17856	11	*Trochammina advena* (59%) *Ammonia* sp. (16%)	
	III	1A 1C	32832	17	*Ammonia* sp. (48%) *Trochammina advena* (34%)	
Cowpen Marsh (N_D recorded on August 10th, 1995)	Upper	1 –16	8610	8	*Jadammina macrescens* (73%) *Trochammina inflata* (10%)	
	Lower	17 –31	7068	30	*Haynesina germanica* (36%)	

(PATIs). PATIs are intervals of time when relatively little change in the foraminiferal assemblage is recorded. These intervals are assumed to coincide with minimal flux in ecological factors influencing temporal turnover. Two or more consecutive peaks in ATIs resulted in PATIs comprised of one sample occasion and indicate periods of prolonged assemblage turnover.

3.4. Conditioned on-boundary index (CoBI)

To assess the proportional contribution of each species to the assemblage's total turnover or change, CoBI was calculated by subtracting the p_i from each PATI straddling the peak ATI, and dividing the absolute value by the ATI value (Eq. (2); Hayek and Wilson, 2013).

$$CoBI = \frac{|p_{i1} - p_{i2}|}{ATI} \quad (2)$$

Hayek and Wilson (2013) defined two types of CoBI. Partial CoBI ($CoBI_p$) was used to define assemblage change exactly at a boundary between PATIs. Thorough CoBI ($CoBI_t$) was used to detect species changes between the total set of sample occasions within two distinct PATIs. Both $CoBI_t$ and $CoBI_p$ require recalculating the ATI value at the boundary. For $CoBI_p$, partial ATI (ATI_p) is calculated between the entire set of sample occasions within the PATI before the boundary (or peaks in ATI_s) and the first sample occasion immediately after the boundary. For $CoBI_t$, thorough ATI (ATI_t) is calculated between the entire set of sample occasions within the two PATIs before and after the boundary. Therefore, when using Eq. (1) for calculating ATI_p, the p_{i1} is the proportional abundance of the ith species in the entire PATI before the boundary, and p_{i2} is the proportional abundance of the ith species in the first sample occasion immediately after the boundary. When using Eq. (1) for calculating ATI_t, the p_{i1} and p_{i2} are the proportional abundances of the ith species in the two PATIs separated by the boundary.

The proportional contribution of each species to the assemblage turnover was assessed by the vector of $CoBI_p$ and $CoBI_t$ values ≥ 0.01. CoBI values > 0.10 indicated those species which provided the greatest contributions to this relative change. A species either increased or decreased across a PATI boundary if p_{i2} - pi_1 were positive or negative, respectively. In Table 3, negative values of p_{i2} - pi_1 were italicized and bold text is used to highlight CoBI values ≥ 0.10.

Table 3
Thorough and partial conditioned on-boundary indices ($CoBI_t$ and $CoBI_p$) of species where CoBI > 0.10 at each location.

CoBI	$CoBI_t$	$CoBI_p$	$CoBI_t$	$CoBI_p$	$CoBI_t$	$CoBI_p$	$CoBI_t$	$CoBI_p$	$CoBI_t$	$CoBI_p$	$CoBI_t$	$CoBI_p$	$CoBI_t$	$CoBI_p$	$CoBI_t$	$CoBI_p$	$CoBI_t$	$CoBI_p$
Caroni Swamp	Metacommunity				Assemblage I						Assemblage II							
PATI	1/2		2/3		1/2		2/3		3/4		1/2		2/3		3/4		4/5	
Ammonia parkinsoniana	0.01	0.01	**0.27**	*0.01*	0.01	0.05	0.02	0.01	**0.29**	0.02	–	–	0.01	0.01	–	0.01	**0.18**	**0.19**
Ammonia tepida	**0.12**	**0.12**	***0.28***	***0.31***	0.04	***0.24***	***0.28***	***0.26***	0.06	0.05	**0.46**	**0.46**	***0.47***	***0.44***	*0.05*	*0.06*	*0.03*	0.03
Ammotium salsum	**0.18**	**0.18**	0.01	0.02	**0.31**	0.02	0.05	0.06	*0.06*	*0.06*	*0.01*	*0.01*	*0.02*	0.02	–	0.07	**0.16**	**0.23**
Arenoparella mexicana	***0.23***	***0.23***	0.04	*0.03*	–	0.03	*0.01*	*0.01*	0.01	–	***0.18***	***0.18***	***0.23***	**0.18**	*0.09*	***0.19***	***0.35***	***0.26***
Miliammina fusca	*0.05*	*0.05*	0.04	0.42	***0.35***	***0.19***	**0.18**	**0.15**	***0.17***	***0.14***	–	–	0.01	0.01	0.08	0.02	0.13	0.06
Trochammina advena	**0.18**	**0.18**	***0.19***	***0.12***	0.06	**0.39**	***0.16***	***0.17***	0.02	**0.27**	*0.07*	*0.07*	0.03	0.01	0.07	–	*0.01*	0.01
Trochammina inflata	–	–	0.08	–	–	–	0.01	–	–	–	*0.02*	*0.02*	–	–	0.3	**0.38**	*0.09*	***0.19***
Trochammina laevigata	***0.16***	***0.16***	*0.02*	0.07	*0.03*	*0.01*	–	0.01	*0.01*	*0.01*	***0.19***	***0.19***	**0.17**	**0.25**	***0.34***	***0.23***	0.01	–

Claxton Bay	Metacommunity				Assemblage II				Assemblage III	
PATI	1/2				2/3				1/2	
Ammonia tepida	***0.13***		***0.18***		**0.21**	0.06	**0.22**	**0.22**	***0.23***	***0.23***	**0.22**	**0.19**
Ammotium salsum	0.2		**0.13**		*0.06*	*0.04*	*0.09*	*0.09*	0.1	0.09	0.17	0.1
Miliammina fusca	*0.04*		*0.03*		*0.01*	*0.01*	*0.01*	*0.01*	–	–	*0.04*	*0.01*
Triloculina oblonga	***0.28***		***0.24***		**0.17**	**0.41**	**0.28**	**0.28**	***0.27***	***0.26***	***0.21***	***0.26***
Trochammina advena	**0.28**		**0.35**		***0.42***	***0.44***	***0.36***	***0.36***	**0.27**	**0.36**	***0.2***	**0.4**

Cowpen Marsh	Metacommunity								Upper assemblage				Lower assemblage					
PATI	1/2		2/3		3/4		4/5		1/2		2/3		1/2		2/3		3/4	
Elphidium earlandi	–	–	*0.01*	0.02	0.02	0.02	*0.01*	0.03	0	0	0	*0.01*	***0.16***	***0.16***	**0.16**	**0.25**	***0.16***	***0.19***
Elphidium excavatum	–	–	–	–	0.02	0.02	0.03	0.03					**0.29**	**0.29**	***0.23***	***0.16***	–	–
Elphidium williamsoni	0.01	0.01	*0.04*	*0.01*	0.04	0.04	0.08	0.01	0.01	0.01	0.02	*0.01*	**0.15**	**0.15**	0.23	0.09	0.24	0.11
Haplophragmoides spp.	**0.32**	**0.32**	***0.24***	***0.37***	**0.23**	**0.23**	***0.32***	–	**0.29**	**0.29**	***0.29***	***0.28***						
Haynesina germanica	0.07	0.07	*0.1*	0.03	0.04	0.04	*0.05*	0.08	*0.01*	*0.01*	*0.02*	0.02	***0.14***	***0.14***	***0.18***	**0.25**	**0.26**	**0.39**
Jadammina macrescens	***0.47***	***0.47***	**0.38**	**0.34**	***0.47***	***0.47***	**0.39**	**0.31**	***0.38***	***0.38***	**0.27**	**0.33**	0.03	0.03	–	*0.04*	*0.03*	*0.03*
Quinqueloculina spp.	0.03	0.03	*0.01*	0.1	0.05	0.05	0.01	0.13	*0.02*	*0.02*	0.05	0.01	*0.08*	*0.08*	0.08	**0.16**	***0.28***	***0.21***
Trochammina inflata	0.01	0.01	*0.11*	*0.01*	0.09	0.09	*0.08*	*0.04*	*0.08*	*0.08*	**0.14**	**0.14**	–	–	0.03	–	–	*0.02*

Bay of Cadiz	Metacommunity				Plot I		Plot III			
PATI	1/2		2/3		1/2		1/2		2/3	
Ammonia tepida	*0.01*	***0.29***	*0.01*	*0.02*	0.03	***0.22***	*0.03*	***0.13***	0.01	0.01
Brizalina spathulata	0.05	**0.12**	0.01	*0.05*	0.05	0.07	*0.01*	*0.06*	-	*0.01*
Cornuspira involvens	*0.01*	*0.05*	0.06	–	**0.18**	*0.04*	-	*0.01*	**0.19**	0.07
Cribroelphidium excavatum	0.06	0.04	*0.02*	*0.08*	0.07	0.01	*0.03*	***0.12***	0.03	*0.06*
Eggerelloides scabrus	0.04	0.01	0.01	*0.04*	0.03	0.01	*0.03*	***0.1***	0.03	0.09
Fisurina lucida	0.01	0.02	0.02	*0.01*	0.06	0.01	*0.01*	*0.03*	0.05	**0.17**
Haynesina germanica	0.05	0.03	0.05	*0.05*	**0.19**	0.04	*0.04*	*0.16*	0.01	*0.08*
Pseudotriloculina laevigata	0.09	**0.29**	*0.04*	*0.08*	**0.19**	**0.16**	*0.01*	*0.06*	0.03	***0.34***
Quinqueloculina seminula	*0*	***0.1***	0.01	-	0.01	***0.12***	*0.01*	*0.05*	0.01	0.01

4. Results

4.1. Caroni Swamp

4.1.1. Foraminiferal metacommunity

The foraminiferal metacommunity at Caroni Swamp had ATI_s that ranged between 0.23 and 1.41 ($x = 0.82$ and $\sigma = 0.28$). Two peaks in ATI_s (where $ATI_s > x + \sigma = 1.10$) occurred between (a) August and September 2011 and (b) December and January 2012 (Fig. 1a). Peak ATI_s occurred two months after the start of the 2011 wet season and end of the same season. One month after the start of the wet season, $ATI_s = 1.10$ between June–July 2011, just failed to meet the control measure for peak ATI_s. Therefore, three PATIs had comparatively low rates of assemblage turnover. PATI-1 spanned the 2011 dry into wet season, PATI-2 enclosed the 2011 late wet season, and PATI-3 comprised all of 2012 to May 2013. Across all PATI boundaries, ATI_t and ATI_p increased (Fig. 1a). Values of $CoBI_t$ and $CoBI_p$ indicate *Ammonia tepida* and *Trochammina advena* were major contributors to assemblage turnovers across all PATI boundaries and fluctuated in phase (Table 3). Between PATI-1 and 2, *A. tepida*, *T. advena* and *Ammotium salsum* increased when *Arenoparella mexicana* and *Trochammina laevigata* decreased. Between PATI-2 and 3, *Ammonia parkinsoniana* increased when *A. tepida* and *T. advena* decreased.

4.1.2. Assemblage I

Assemblage I of Caroni Swamp had ATI_s that ranged between 0.00 and 2.00 ($x = 0.91$ and $\sigma = 0.42$). Three peaks in ATI_s (where $ATI_s > x + \sigma = 1.33$) occurred between (a) May and June 2011, (b) January and February 2012, and (c) August and September 2012 (Fig. 1b). The first two peaks coincided with the start of the 2011 wet and 2012 dry seasons and the third peak occurred two months after the start of the 2012 wet season. Between March and April, $ATI_s = 1.26$ just failed to attain the control value for peak ATI_s. Therefore, PATI-1, 2, and 3 enclosed periods of mainly dry, wet and dry conditions, respectively. Across all PATI boundaries ATI_p decreased, but ATI_t increased from PATI-1 to 2 to 3 and decreased from PATI-3 to 4 (Fig. 1b). *Ammonia becarrii, A. tepida, A. salsum, Miliammina fusca* and *T. advena* were influential to all assemblage turnovers (Table 3). From dry to wet conditions in 2011 (PATI-1 to 2), *A. tepida* and *M. fusca* decreased when *A. salsum* and *T. advena* increased. From wet to dry conditions (PATI-2 to 3), *M. fusca* increased when *A. tepida* and *T. advena* decreased. Early 2012 wet season (PATI-3 to 4), *M. fusca* decreased when *T. advena* increased.

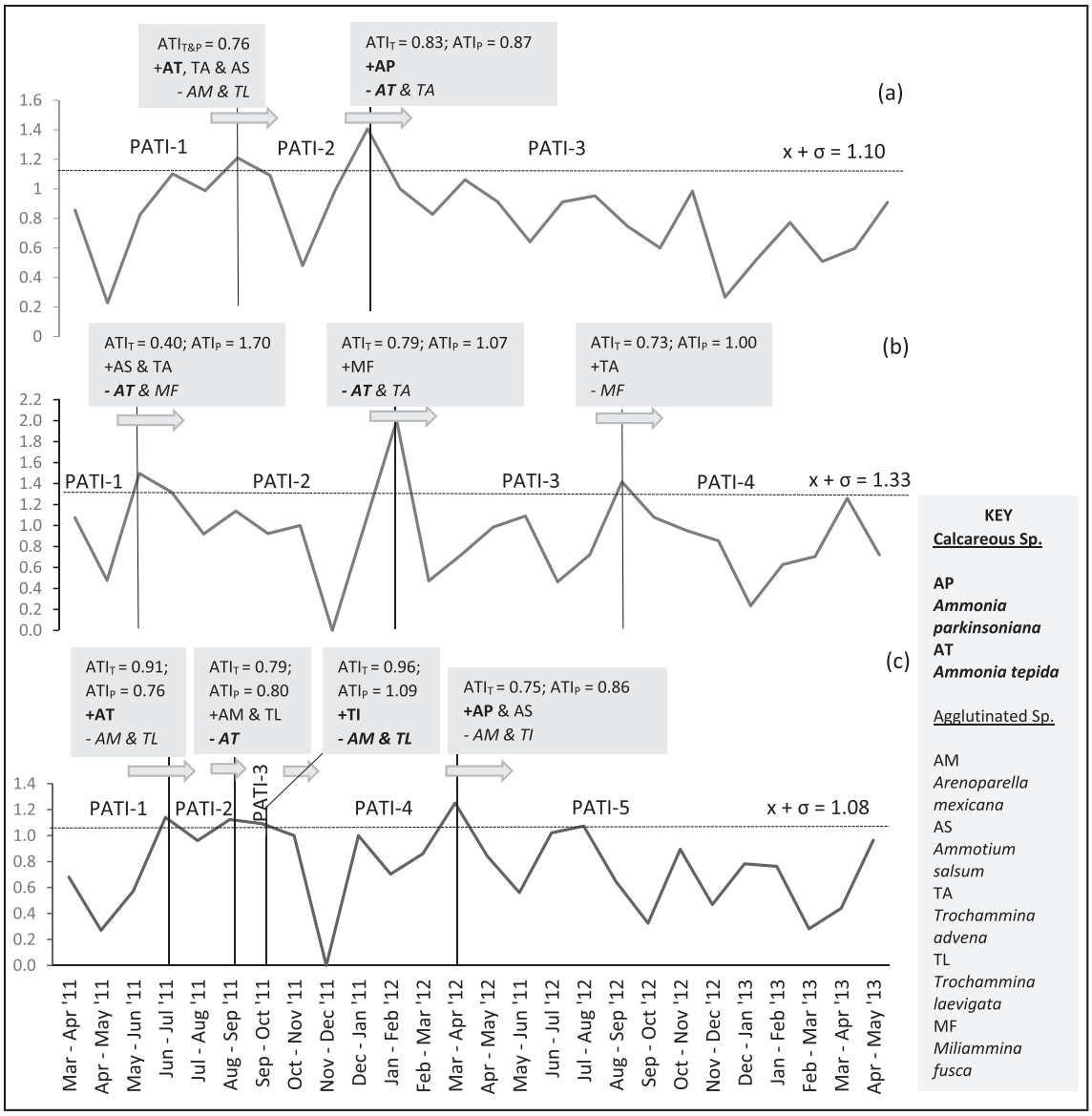


Fig. 1. Assemblage turnover indices of Caroni Swamp (a) metacommunity (b) assemblage I and (c) assemblage II, illustrating peak ATI$_s$ values (>x + σ) and PATIs in between.

4.1.3. Assemblage II

Assemblage II of Caroni Swamp had ATI$_s$ that ranged between 0.00 and 1.25 (x = 0.76 and σ = 0.32). Four peaks in ATI$_s$ (where ATI$_s$ > x + σ = 1.08) occurred between (a) June and July, (b) August and September, (c) September and October 2011, and (d) March and April 2012 (Fig. 1c). The first peak occurred one month after the start of the wet season. The following two peaks occurred consecutively, representing prolonged assemblage turnover during the mid wet season. The fourth peak occurred two months after the start of the dry season. Between July and August, ATI$_s$ = 1.07 just failed the control measure for peak ATI$_s$. Across all PATI boundaries, ATI$_t$ fluctuated in a saw-tooth pattern (Fig. 1c). ATI$_p$ increased gradually across all PATI boundaries except PATI-4 to 5 (Fig. 1c). *Ammonia tepida*, *A. mexicana*, *T. advena* and *T. laevigata* were major contributors to all assemblage turnovers (Table 3). Early 2011 wet season (PATI 1 to 2) *A. tepida* increased when *A. mexicana* and *T. laevigata* decreased (Fig. 1c). Two months later (PATI-2 to 3) this pattern was reversed, and one month later (PATI-2 to 3) *Trochammina inflata* increased when *A. mexicana* and *T. laevigata* decreased. These three major assemblage turnovers all occurred during wet conditions. The last major assemblage turnover occurred two months after the start of the dry season (PATI-4 to 5) when *A. parkinsoniana* and *A. salsum* increased, while *A. mexicana* and *T. inflata* decreased.

4.2. Claxton Bay

4.2.1. Foraminiferal metacommunity

The foraminiferal metacommunity at Claxton Bay had ATI$_s$ that ranged between 0.08 and 0.56 (x = 0.33 and σ = 0.14). Two peaks in ATI$_s$ (where ATI$_s$ > x + σ = 0.47) occurred between (a) September and October and (b) November and December 2012, towards the end of the wet season (Fig. 2a). Across all PATI boundaries ATI$_t$ and ATI$_p$ increased (Fig. 2a). During the first major assemblage turnover *A. salsum* and *T. advena* increased when *A. tepida* and *Triloculina oblonga* decreased (Table 3). During the second major assemblage turnover *A. tepida* and *T. oblonga* increased when *T. advena* decreased. When agglutinated species increased, calcareous

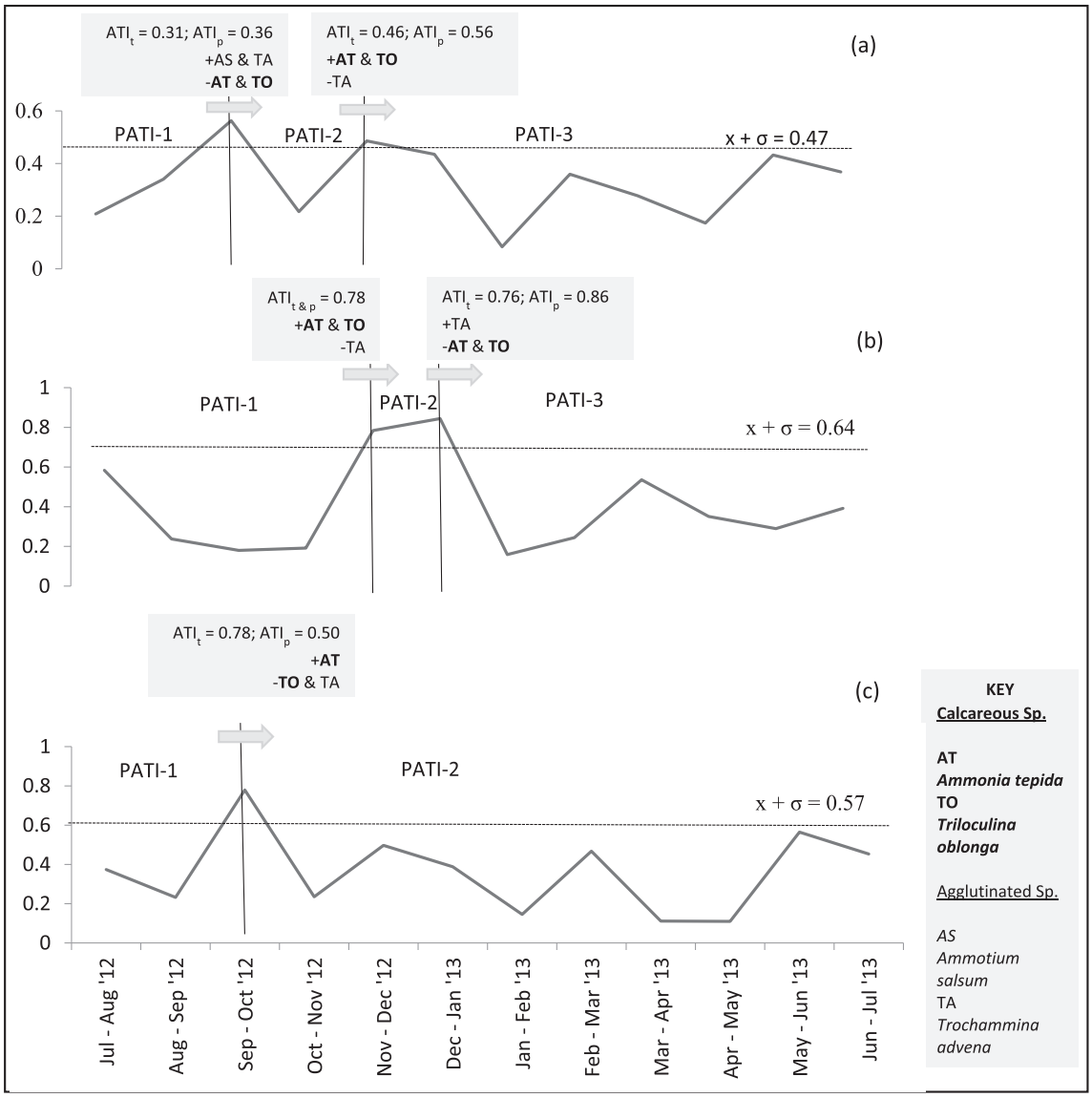


Fig. 2. Assemblage turnover indices of Claxton Bay (a) metacommunity (b) assemblage II and (c) assemblage III, illustrating peak ATI_s values (>x + σ) and PATIs in between.

species decreased, and vice versa (Fig. 2a).

4.2.2. Assemblage II

Assemblage II of Claxton Bay had ATI_s that ranged between 0.16 and 0.84 (x = 0.40 and σ = 0.24). Two consecutive peaks in ATI_s (where $ATI_s > x + \sigma = 0.64$) occurred between (a) November and December 2012, and (b) December 2012 and January 2013 (Fig. 2b), indicating prolonged assemblage turnover at the end of the wet season. At this time, ATI_T decreased but ATI_P increased and *Trochammina advena*, *T. oblonga* and *A. tepida* were major contributors (Fig. 2b). At the end of the wet season, from PATI-1 to 2, A. tepida and *T. oblonga* increased when *T. advena* decreased (Table 3). During the transition from wet to dry conditions, PAT-2 to 3, *T. advena* increased when *A. tepida* and *T. oblonga* decreased. Agglutinated and calcareous species fluctuated in phase and in opposition to each other (Fig. 2b).

4.2.3. Assemblage III

Assemblage III of Claxton Bay had ATI_s that ranged between 0.11 and 0.78 (x = 0.36 and σ = 0.20). One peak ATI_s (where $ATI_s > x + \sigma = 0.57$) occurred between September and October 2012 (Fig. 2c), mid wet season. *Ammonia tepida* increased when *T. oblonga* and *T. advena* decreased (Table 3), such that agglutinated and calcareous species did not fluctuate in phase (Fig. 2c) as in the metacommunity (Fig. 2a) and assemblage II (Fig. 2b).

4.3. Cowpen Marsh

4.3.1. Foraminiferal metacommunity

The foraminiferal metacommunity at Cowpen Marsh had ATI_s that ranged between 0.10 and 0.66 (x = 0.32 and σ = 0.17). Four peaks in ATI_s (where $ATI_s > x + \sigma = 0.49$) occurred between the (a) 12th and 28th of June, (b) 28th and 12th of July 1995, (c) 5th and 20th of January, and (d) 20th and 4th of February 1996 (Fig. 3a). The first and last two peaks occurred consecutively, representing two prolonged assemblage turnovers one month after the start of summer and winter. Values of ATI_t and ATI_p fluctuated in a saw-tooth pattern across all PATI boundaries (Fig. 3a). Only two species of the metacommunity had major contributions to the turnovers: *Jadammina macrescens* and *Haplophragmoides* spp. (Table 3).

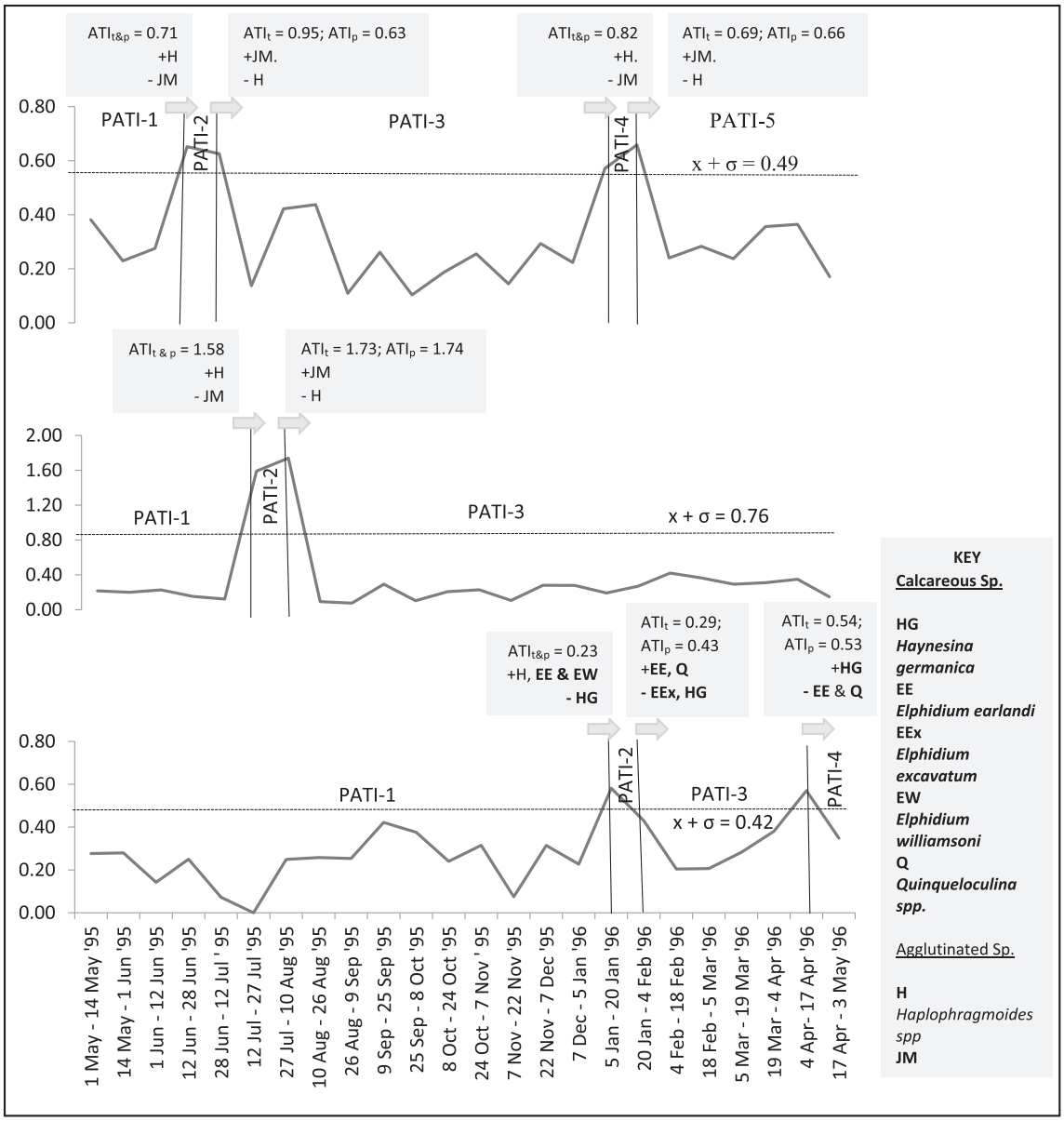


Fig. 3. Assemblage turnover indices of Cowpen Marsh (a) metacommunity (b) upper and (c) lower assemblages, illustrating peak ATI_s values ($>x + \sigma$) and PATIs in between assemblage turnovers across all PATI.

During both prolonged assemblage turnovers *Haplophragmoides* spp. increased and decreased when *J. macrescens* decreased and increased (Fig. 3a).

4.3.2. Upper foraminiferal assemblage

The upper assemblage of Cowpen Marsh had ATI_s that ranged between 0.08 and 1.74 ($x = 0.34$ and $\sigma = 0.42$). Two consecutive peaks in ATI_s (where $ATI_s > x + \sigma = 0.76$) occurred between the (a) 12th and 27th of July and (b) 27th and 10th of August 1995 (Fig. 3b). This prolonged assemblage turnover coincided with the start of summer. Across all PATI boundaries, ATI_t and ATI_p increased (Fig. 3b). As observed in the metacommunity, *J. macrescens* and *Haplophragmoides* spp. were major contributors to the prolonged assemblage turnover and fluctuated in opposition (Table 3; Fig. 3b).

4.3.3. Lower foraminiferal assemblage

The lower assemblage of Cowpen Marsh had ATI_s that ranged between 0 and 0.58 ($x = 0.28$ and $\sigma = 0.14$). Three peaks in ATI_s (where $ATI_s > x + \sigma = 0.42$) occurred between the (a) 5th and 20th of January, (b) 20th and 4th of February and (c) 4th and 17th of April 1996 (Fig. 3c). At the start of autumn, $ATI_s = 0.42$ between the 9th and 25th of September, just failed the control measure for peak ATI_s. Therefore, little change was recorded in the lower assemblage from May to December of 1995 (PATI-1). Prolonged assemblage turnover occurred at the beginning of winter (from PATI-1 to 2 to 3) and spring (PATI-3 to 4). Across all boundaries ATI_t and ATI_P increased (Fig. 3c). Mainly calcareous species of Haynesina, Elphidium and Quinqueloculina contributed the most to major turnovers of the lower assemblage (Table 3; Fig. 3c). Prolonged assemblage turnover at the start of the winter was characterized by an increase in *Haplophragmoides* spp., *Elphidium earlandi* and *Elphidium williamsoni* and decrease in *Haynesina germanica*. This was immediately followed by an increase in *E. earlandi* and *Quinqueloculina* spp. when *Elphidium excavatum* and *Haynesina germanica* decreased.

Only at the start of the spring did *Haynesina germanica* increase when *E. earlandi* and *Quinqueloculina* spp. decrease.

4.4. Bay of Cádiz

4.4.1. Foraminiferal metacommunity

The ATI_s values of the metacommunity at Bay of Cádiz, ranged between 0.87 and 0.52 ($x = 0.70$ and $\sigma = 0.14$). Two peaks in ATI_s (where $ATI_s > x + \sigma = 0.84$) occurred between (a) July and September 2008 and (b) November and December 2008 (Fig. 4a), which coincided with seasonal changes from summer to autumn, and autumn to winter, respectively. At the start of spring, $ATI_s = 0.83$ between February and May, just failed to meet the criterion for peak ATI_s. Across all PATI boundaries, ATI_t and ATI_p increased (Fig. 4a). From summer to autumn (PATI-1 to 2) *A. tepida* and *Q. seminula* decreased when *B. spathulata* and *P. laevigata* increased (Table 3). From autumn to winter, PATI-2 to 3, no species had CoBI values > 0.10 but $CoBI_p$ values indicate most species declined.

4.4.2. Plot I

The foraminiferal assemblage within plot I at Bay of Cádiz had ATI_s that ranged between 0.58 and 1.15 ($x = 0.88$ and $\sigma = 0.18$). One peak in ATI_s (where $ATI_s > x + \sigma = 1.06$) occurred between July and September 2008 (Fig. 4b). PATI-1 to 2 represents the transition from summer to autumn. Major contributors to the assemblage turnover from PATI-1 to 2 were *Pseudotriloculina laevigata, Cornuspira involvens and H. germanica*, which increased and *Ammonia tepida* and *Quinqueloculina seminulina*, which decreased (Table 3).

4.4.3. Plot II

The foraminiferal assemblage within plot II at Bay of Cádiz had ATI_s that ranged between 0.47 and 1.04 ($x = 0.86$ and $\sigma = 0.19$). The greatest ATI_s value (1.04) was recorded between February and May

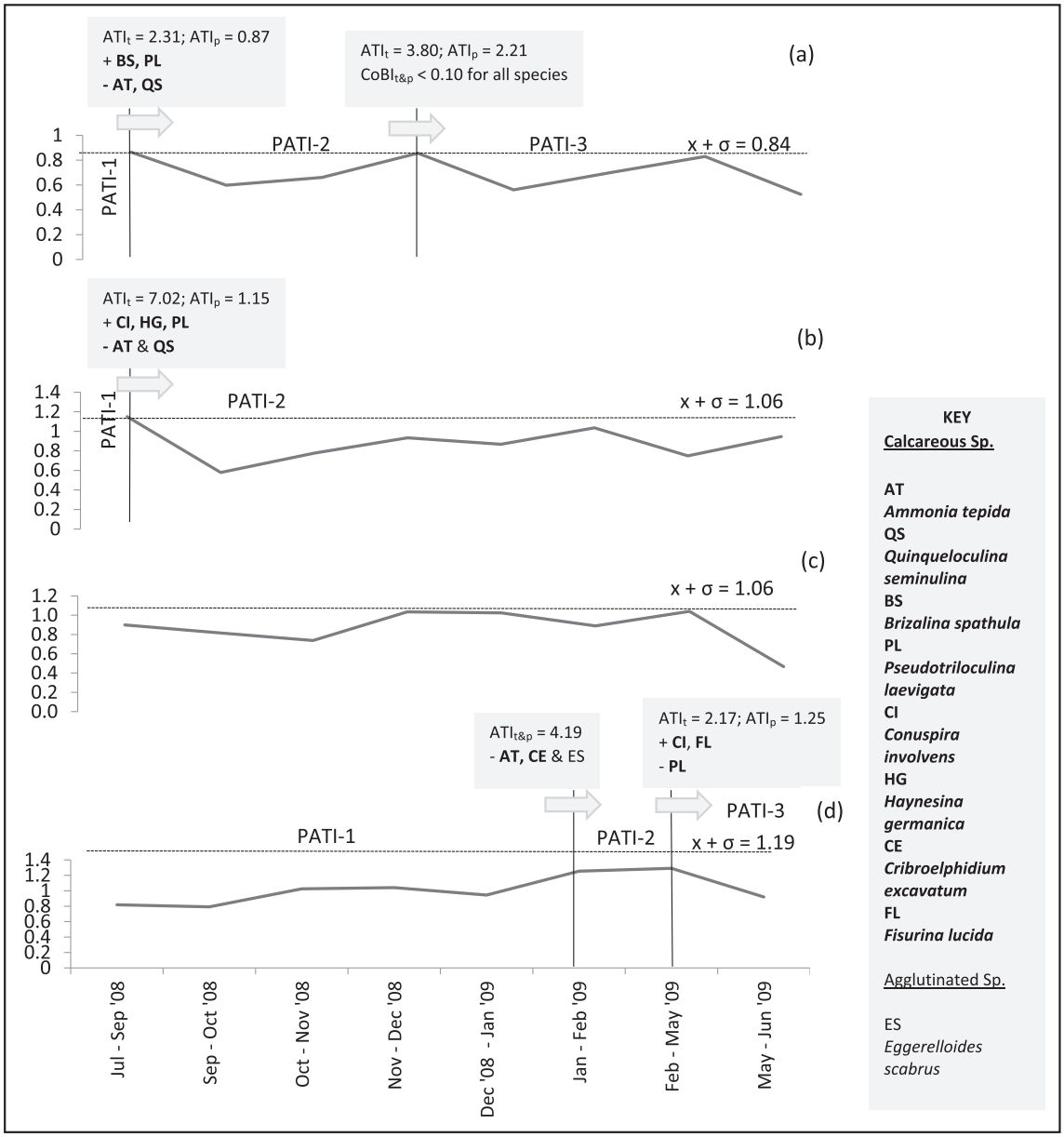


Fig. 4. Assemblage turnover indices of Bay of Cádiz (a) metacommunity (b) plot I (c) plot II and (d) plot III, illustrating peak ATI_s values ($>x + \sigma$) and PATIs in between.

2009, between winter and spring seasons (Fig. 4c). However, this just failed the criterion for peak ATI_s (where $ATI_s > x + \sigma = 1.06$). Species fluctuations were relatively consistent throughout the sample period with no major assemblage turnovers recorded, PATI boundaries were absent and CoBI values were not calculated.

4.4.4. Plot III

The foraminiferal assemblage of plot III at Bay of Cádiz had ATI_s that ranged between 0.79 and 1.29 ($x = 1.01$ and $\sigma = 0.18$). Two peaks in ATI_s (where $ATI_s > x + \sigma = 1.19$) occurred between (a) January and February 2009 and (b) February and May 2009 (Fig. 4d). As such, prolonged assemblage turnover coincided with the start of winter when ATI_t and ATI_p decreased. Species contributing to the first turnover, *A. tepida, Cribroelphidium excavatum* and *Eggerelloides scabrous*, decreased. After which, *Conuspira involvens* and *Fissurina lucida* increased when *Pseudotriloculina laevigata* decreased.

5. Discussion

Hayek and Wilson (2013) first applied the ATI and CoBI indices to Neogene foraminifera as a sequence stratigraphic tool, to examine whether glacial – interglacial cycles were marked by species-level changes within community composition. Here, the ATI and CoBI indices are demonstrated to be equally useful in determining temporal assemblage turnovers using time series of live foraminiferal population densities. At tropical locations, major assemblage turnovers which occurred within 2 months of January or May (start and end of the dry season) and June or December (start and end of the wet season) were considered coincident with seasonal change to account for transitions between seasons. At Caroni Swamp, nine major turnovers were recorded for the metacommunity and assemblages combined, of which five coincided with seasonal change and four occurred mid-season. At Claxton Bay, five major turnovers were recorded for the metacommunity and assemblages combined, of which three coincided with seasonal change from wet to dry conditions and two occurred mid wet season. At Cowpen Marsh, all of the nine recorded major turnovers coincided with seasonal change. Two prolonged assemblage turnovers of the metacommunity coincided with the start of summer and winter. The summer turnover was repeated in the upper assemblage, and the winter turnover in the lower assemblage. Similarly at Bay of Cadiz, all three major assemblage turnovers coincided with seasonal change at the end of summer and start of winter.

The Orinoco River discharge is highest from July to October (López et al., 2013). Its arrival in the Gulf of Paria lags by one month due to travel time (Subrath-Ali et al., 2013). Therefore, the effects of the low salinity plume would be greatest in the Gulf of Paria between August and November. At Caroni Swamp and Claxton Bay, the major assemblage turnovers which occurred mid-seasons were coincident with the arrival and disappearance of the plume between August/September and November/December. Orinoco River water is slightly acidic, pH = 6.8 (Lewis and Weibezahn, 1981), and may lower the sediment pH in intertidal areas. This has been recorded elsewhere in the tropics to cause dissolution of calcareous specimens (Green et al., 1993; Debenay et al., 2004). Previous statistical comparisons of the seasonal foraminiferal densities at Claxton Bay indicated that the calcareous species significantly increased during dry conditions and declined during wet conditions (Costelloe and Wilson, 2015). Within the metacommunity and assemblage II of Claxton Bay, calcareous and agglutinated species fluctuated in opposition. Only in the metacommunity did calcareous species decline during wet conditions and increase during dry conditions. In assemblage II there was a period of prolonged assemblage turnover between the end of the wet season and start of the dry season, when calcareous species increased and decreased. Therefore, the analyses of CoBI values for calcareous species which contributed to major turnovers does not provide a consistent pattern that would be suggestive of adverse conditions, such as decreased sediment pH, as a result of the Orinoco plume during the wet season.

Across all PATI boundaries, species fluctuated in saw-toothed patterns typical of first-order population dynamics governed by intraspecific competition (Berryman and Kindlmann, 2008). The carrying capacity is the number of species which an area can support while meeting the needs of all individuals and when achieved represents equilibria (Kashiwai, 1995). An increase in nutrients or food supply to a community can result in large overshoots checked by intraspecific competition to obtain equilibria (Berryman and Kindlmann, 2008). In the waters surrounding Trinidad, the seasonal Orinoco plume enhances stratification and nutrient inputs that increase biological productivity (Hu et al., 2004). Increased biological productivity as a result of coastal upwelling has produced seasonal variations in planktonic foraminifera of the nearby Cariaco Basin, Venezuela (Tedesco and Thunnnel, 2003). At temperate latitudes, sediment macro algal blooms and offshore phytoplankton blooms occur due to thermal stratification in the spring and summer months (Swallow, 2000; Murray and Alve, 2000; Alve and Murray, 2001). Interspecific competitive patterns are notably displayed by two or more species in the following instances:

(1) *T. advena* and *M. fusca* of Caroni Swamp assemblage I (Fig. 1b) fluctuated in opposition across all PATI boundaries.
(2) *A. tepida* and *T. oblonga* fluctuated in opposition to *T. advena* in the metacommunity and assemblage II of Claxton Bay (Fig. 2a and b). These were the only three species which contributed greatly to all major assemblage turnovers.
(3) *Haplophragmoides* spp. and *J. macrescens* were the only considerable contributors to major turnovers of the Cowpen Marsh metacommunity and upper assemblage and fluctuated in opposition across all PATI boundaries (Fig. 3a and b).

At Cowpen Marsh, assemblage turnovers were influenced by the dominant species of the metacommunity, upper assemblage (*J. macrescens* and *Haplophragmoides* spp.) and lower assemblage (*H. germanica*). Other sub-dominant species of the lower assemblage also contributed to assemblage turnovers (*E. earlandi, E. williamsoni, E. excavatum* and *Quinqueloculina* spp.). The average lifespan of agglutinated foraminifera ranges from 1.3 to 13 years at South Island New Zealand, where Hayward et al. (2014) recorded no evidence for seasonal blooms. At high marsh elevations, *Haplophragmoides wilberti* may live for 3 years and life spans were shorter for those at shallower infaunal depths and less stressful conditions (Hayward et al., 2014). At Cowpen Marsh, fluctuations in relative abundances of *Haplophragmoides* spp. reflect shorter life spans (monthly or biweekly). Shorter lifespans may be a byproduct of seasonal fluctuations in food supply that increase intraspecific competition through large population blooms that overshoot the carrying capacity equilibria. Alternatively, populations not affected by seasonal fluctuations, such as those of Hayward et al. (2014), may be more stable and have longer life spans. In this way seasonality is a natural environmental stress affecting foraminiferal population dynamics and should be separated from other stresses related to anthropogenic activity or long-term climatic change.

At Bay of Cádiz, the metacommunity (sum of all three plots) confirmed that seasonal assemblage turnovers occurred at the end of summer and start of winter. However, there was a considerable degree of inconsistency in temporal variability of the foraminiferal assemblages between plots spaced 10–15 m apart. Major

assemblage turnovers occurred at the end of summer from plot I; winter from plot III; and were completely absent from plot II. This confirms the importance stressed by others (Swallow, 2000; Murray and Alve, 2000; Buzas et al., 2002; Schönfeld et al., 2012) on replicate sampling to overcome the patchy distribution of benthonic foraminifera in the sediment. Patchiness occurs on scales of centimeters, between replicated samples, and meters, between stations or assemblages (Schafer, 1971; Buzas et al., 2002; Bouchet et al., 2012).

6. Conclusions

The ATI and CoBI are relatively novel indices for quantitatively identifying major assemblage turnovers and contributing species. The relationships between intertidal foraminiferal populations are explored by applying these indices to time series data sets of the live species proportional abundances. At tropical locations in the Southern Caribbean, seasonal population dynamics of foraminiferans have been associated with the effects of increased fluvial runoff during wet seasons. Intertidal foraminiferans of Trinidad displayed major assemblage turnovers which were coincident with seasonal rainfall and maximum outflow of the Orinoco River (Venezuela) during the wet season. Dominant *Ammonia spp.*, *T. oblonga*, *A. salsum* and *T. advena;* and subdominant *M. fusca* and *T. laevigata* contributed the most to assemblage turnovers. Species fluctuations during seasonal turnovers would suggest biotic controls, such as interspecific competition, were more influential in determining species population blooms and busts than abiotic controls, such as sediment pH.

At temperate Cowpen Marsh and Bay of Cádiz, major assemblage turnovers were coincident with either the start or end of summer and beginning of winter. At Cowpen Marsh, the summer assemblage turnover was recorded in populations at higher elevations only and were led by dominant *J. macrescens* and rarer *Haplophragmoides* spp. At lower elevations, winter assemblage turnovers were led by dominant *H. germanica*. Seasonal assemblage turnovers at Bay of Cádiz were detected by the cumulative analysis of replicate samples collected within 3 plots spaced 10 and 15 m apart. Separate analysis of each plot gave inconsistent results, which highlights the need for replicate samples from multiple stations to provide a complete representation of the foraminiferal metacommunities. The ATI and CoBI methods were useful for identifying temporal assemblage turnovers of species interrelationships which coincided with seasonal change and indicated competitive trends.

Data availability

Data used in this study can be obtained directly by contacting the authors.

Team list

The authors listed comprise the team which contributed to the analysis of published data here.

Author contribution

Data was collected by A. Costelloe from Caroni Swamp and Claxton Bay; and by B. Horton from Cowpen Marsh. A. Costelloe was responsible for applying the assemblage turnover index (ATI) and conditioned-on-boundary index (CoBI) to time series data sets of live foraminiferal densities. The methods were guided and reviewed by B. Wilson and L-A Hayeck.

Competing interests

The authors declare that they have no conflict of interest.

Disclaimer

Authors contributed to this article in each personal capacity and are in agreement with the final presentation submitted to Estuarine, Coastal and Shelf Science. The analysis presented has not been previously published and is an original work compiled by the authors using data previously published.

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